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THE INFLUENCE OF THE CEREBRAL CORTEX
ON THE LARYNX.

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II. *The Influence of the Cerebral Cortex on the Larynx.*

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(From the Pathological Laboratory of University College, London.)

Communicated by Professor VICTOR HORSLEY, F.R.S.

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CONTENTS.

	Page.
I. Introduction	60
II. History	61
III. Plan of Experimentation	62
1. Operative Procedure	62
2. Electrical Excitation	63
3. Graphic Records	63
4. Anæsthesia	64
IV. Certain Preliminary Considerations	64
V. The Dog	67
1. Adduction of the Vocal Cords	67
2. Abduction of the Vocal Cords	69
3. Acceleration of the Movements of the Vocal Cords	70
4. A Clonic Adductor Effect on the Cords	71
5. Arrest of the Vocal Cords in Adduction	72
6. Arrest of the Vocal Cords in Abduction	73
7. Intensification and Acceleration of the Movements of the Vocal Cords	73
8. SPENCER'S Area of Arrest of Respiration	74
VI. The Cat	74
1. Adduction of the Vocal Cords	75
2. Abduction of the Vocal Cords	75
3. Acceleration of the Movements of the Vocal Cords	76
4. A Clonic Adductor Effect on the Cords	77
5. Arrest of the Vocal Cords in Adduction	77
6. Arrest of the Vocal Cords in Abduction	77
7. Intensification and Acceleration of the Movements of the Vocal Cords	78
8. SPENCER'S Area of Arrest of Respiration	79
VII. Discussion of Results	79

I. *Introduction.*

I HAVE much pleasure in thanking Professor VICTOR HORSLEY for allowing me to conduct the experiments which form the subject of this paper at the Pathological Laboratory of University College.

It has always appeared to me contrary to the best established facts with regard to the cerebral localisation of motor processes that some abduction of the vocal cords should not be represented in the cerebral cortex. That abduction should be less powerfully represented in the cortex than adduction seemed clear, but that there should be no centre at all to subserve this function in the cerebral cortex seemed strange. I therefore decided to test the matter on the lines suggested to me by Dr. HUGHLINGS JACKSON in connection with a recent investigation of eye movements, when, after excluding the possibility of the lateral movements of the eyes to the opposite side from the hemisphere stimulated taking place, by dividing the muscles which bring about these movements, I found that it was possible to evoke many other movements of the eyes which hitherto could not be obtained. The conclusion which appeared warranted by these results was that the lateral movements of the eyes are so powerfully represented in the cerebral cortex that they overpower all other movements under normal circumstances.

It seemed quite possible that abduction of the vocal cords is in reality represented in the cerebral cortex, but that adduction is so much more powerfully represented that it is impossible to obtain a stimulus strong enough to evoke abduction without its diffusing to the more powerful adductor centre, which is presumably situated at no great distance from that for abduction.

Taking advantage of my previous observations, that it was possible to separate in the recurrent laryngeal nerve the bundle of abductor from that of adductor fibres,* I came to the conclusion that if, in an animal excitation of whose cerebral cortex only yielded adduction of the vocal cords, I were to divide the adductor fibres of the recurrent laryngeal nerve, without injury to the abductor fibres, it might be possible to evoke the movement of abduction of the vocal cords from the cerebral cortex of the same animal by exciting some area in close proximity to that excitation of which resulted in the movement of adduction before.

During the course of these experiments I was led to investigate other points in connection with the central innervation of the larynx, notably some points relating to the state of the laryngeal apparatus, when SPENCER's area for arrest of respiration† was excited. Inasmuch as I am at present engaged in a more extended inquiry on the correlation of the respiratory and laryngeal central nervous mechanisms, in conjunction with Mr. SPENCER, I will only refer to the effects on the vocal cords without regard to the respiratory movements of the thorax, although many of my

* 'Proc. Roy. Soc.,' 1892.

† SPENCER, 'Phil. Trans.,' 1894.

contentions can only be satisfactorily proved by such an investigation as the joint one to which I have just referred.

II. *History.*

BOUILLAUD* destroyed the frontal lobes in dogs by means of a drill, or the cautery, after which the animals did not bark, but whined when disturbed.

FERRIER† was the first experimenter who obtained any evidence of the representation of laryngeal movements in the cerebral cortex, as shown by the results of electrical stimulation. He obtained barking when the electrodes were applied to the lower portion of the anterior composite gyrus from area (9) in his figure.

DURET‡, from ablation and compression experiments, came to the same conclusion.

H. KRAUSE§ was, however, the first to find the focus in the dog's brain excitation of which resulted in closure of the glottis, as brought about by bilateral adduction of the vocal cords; the focus being the isthmus of the præcrucial gyrus.

FRANÇOIS FRANCK|| observed that during an epileptic convulsion, induced by cortical stimulation, the glottis is closed during the tonic stage, whereas during the clonic stage the cords move in conjunction with the movements of the respiratory muscles of the thorax and abdomen.

MASINI¶, from excitation and ablation experiments in dogs, concluded that the movement of adduction of the vocal cords is represented over the whole motor region, but maximally so in the centres for the movements of the soft palate and tongue. While with strong currents he obtained bilateral adduction, with weak he obtained movement of the opposite vocal cord first, followed later by slower movement of the cord on the side stimulated.

ARONSOHN** could not decide whether the adductor movements of the vocal cords which he obtained were due to the excitation of the brain or not.

HORSLEY and SEMON†† in an elaborate investigation of the central motor innervation of the larynx, conducted in cats, dogs, and monkeys, obtained the following results. As their results in cats correspond more or less with those obtained in dogs, with one important exception, it will suffice if we state that the cat was the only animal from whose cerebral cortex they were able to evoke pure abduction of the vocal cords in the adult animal. In their investigations in the adult dog they

* BOUILLAUD, 'Journ. hebd. de Méd.,' Paris, 1830, vi., p. 527.

† FERRIER, 'Functions of the Brain,' 1st ed., 1876.

‡ DURET, 'Traumatismes cérébraux,' 1878, p. 142.

§ KRAUSE, 'Arch. für Anat. und Physiol., Physiol. Abth.,' 1884.

|| FRANCK, 'Leçons sur les Fonctions Motrices du Cerveau,' Paris, 1887, p. 146.

¶ MASINI, 'Arch. Ital. di Laryngol.,' Napoli, April, 1888, p. 45.

** ARONSOHN, 'Deutsch. Med. Woch.,' 1888.

†† HORSLEY and SEMON, 'Phil. Trans.,' 1890, p. 187.

confirmed KRAUSE's observation as to the chief focus of adduction, but showed that the movement could also be obtained in lessened degree from a wider area. They were never able to obtain pure abduction in the adult dog, although they explored the whole of the frontal lobe on its orbital and external surfaces completely. Acceleration of respiration was obtained from a focus just above the adductor centre, occupying the middle of the lower third of the præcrucial gyrus. Intensification of the movements of the cords was obtained from the sigmoid gyrus, opposite the lower or outer end of the crucial sulcus, most markedly from the lower end of the posterucial gyrus, at which point the intensification was occasionally accompanied by slowing.

In the monkey the area excitation of which evoked adduction of the vocal cords was at the lower extremity of the ascending frontal gyrus just behind the lower end of the præcentral sulcus. During epilepsy there was adduction in the tonic stage, and sometimes a confusion between adduction and respiratory (?) abduction; in the clonic stage the movement of adduction alone occurred in single spasms.

MOTT* states that in attempting to differentiate an abductor centre in the cerebral cortex he discovered no new facts. He confirmed KRAUSE's observation that after ablation of the adductor centre on both sides the animal is still able to bark. He also confirmed the observation of HORSLEY and SEMON that excitation of the laryngeal centre on one side after extirpation of that on the other, results in bilateral movements of the vocal cords.

MASINI† found that in dogs narcotised with morphia, a crystal of cocain placed on the cortical laryngeal centre, or a solution of cocain injected into the substance of the cortex, produced first, slow adductor movements of the opposite vocal cord, and absolute paresis of it in five minutes.

III. *Plan of Experimentation.*

1. *Operative Procedure.*—After the animal was anaesthetised, tracheotomy was always performed and a glass cannula inserted into the distal end of the transversely divided trachea. The free end of the cannula communicated with a short rubber tube, connected with a funnel in which was placed some cotton-wool saturated with ether, the vapour from which was thus inhaled by the animal. A flap was cut from the front of the proximal end of the divided trachea, and gently raised so as to expose the larynx from below, and care was taken not to exert undue traction on the parts for reasons detailed in a former paper.‡ In one series of experiments, the vocal cords were thus directly observed while the cerebral cortex was being excited; but in another series of experiments the movements of the vocal cords were graphically

* MOTT, 'Brit. Med. Journ.,' 1890, p. 1124.

† MASINI, 'Riv. di Pat. e Ter.,' etc., 1894, No. 2.

‡ *Loc. cit.*

recorded, in which case a small india-rubber bag, slightly constricted at its middle, closed at one end and communicating with a tube at the other, was inserted between the vocal cords from below.

The greatest care was taken to detach all surrounding parts from the trachea before tracheotomy was performed in order to avoid any possible injury to either recurrent laryngeal nerve. In certain of the experiments each recurrent nerve was carefully separated from the surrounding loose connective tissue prior to Faradic excitation of the nerves. A subsequent procedure in many of the experiments consisted in separating the abductor from the adductor bundle of fibres in the trunk of the nerve; a fine ligature was gently passed round each, and the greatest care observed in raising them into the air before stimulating them with the induced current. Having thus ascertained which were the abductor and which the adductor fibres, the latter were divided transversely in one or both nerves, as the case might be. In later experiments the plan of passing a ligature round each bundle of fibres and exciting the fibres with the induced current was abandoned as superfluous, as the two sets of fibres could be distinguished from each other with great certainty from their respective positions and course at their distribution. The abductor fibres are situated on the inner, while the adductors are on the outer side of the nerve.

In exposing the anterior part of one cerebral hemisphere, the eye on that side was either excised or its contents evacuated (HITZIG). The zygomatic arch with the muscles attached to it was removed, as was the coronoid process of the inferior maxilla. These preliminaries allowed of free exposure of the cerebral hemisphere on its external and orbital surfaces, the bone being removed piecemeal by means of bone forceps. All bleeding from the bone was arrested by means of wax.

The dura mater was only opened when all was ready to proceed with the excitation of the cortex; and throughout the experiment the cortex was freely bathed with normal saline solution at blood-heat, and carefully protected from the cooling influence of the atmosphere, except at such times that the electrodes were about to be applied to any spot on the surface of the hemisphere, when this was carefully dried, without exerting any pressure on the cortex.

2. *Electrical Excitation.*—The excitation of the recurrent laryngeal nerve, or of the cerebral cortex, was by means of electrodes whose fine platinum points were fixed about 2 millims. apart. These were connected by means of insulated wires to the secondary coil of a Du Bois-Reymond inductorium, supplied by a single bichromate cell, except in those cases in which graphic records of the movements of the vocal cords were taken, in which case three bichromate cells were used on account of the resistance of the electrical signals placed in the circuit.

3. *Graphic Records.*—The small india-rubber bag which was inserted between the vocal cords communicated with a MAREY'S tambour by means of an india-rubber tube and the writing point connected with the tambour recorded on the blackened surface of a HÜRTHE'S kymographion. The rate of movement of this was measured by a

metronome beating seconds and recording on the blackened surface by an electromagnet. An electromagnet also served to indicate the time during which the stimulus was applied. The recording points of the tambour and of the electromagnet indicating the duration of the stimulus were kept as nearly as possible vertically in line.

4. *Anæsthesia*.—Ether was the anæsthetic agent exclusively employed, and the animal was kept under its influence throughout the whole of the experiment, at the termination of which it was invariably killed while still under the influence of the narcotic.

The part played by the influence of the anæsthetic in experiments such as those which I am about to record is so important that I feel compelled to insist on this, in spite of the fact that others (HOOPER, SEMON and HORSLEY) have recognised its importance before me, for there are unfortunately still those who pay no regard to the degree of narcosis, a fact which accounts for much of the contradictory results which have been obtained. It is of the greatest importance that we should carefully note the depth of anæsthesia at the moment of excitation of any given area of the cerebral cortex, for there can be no question that the differentiating effect of ether is such that totally different effects may be obtained from the same focus at different stages of narcosis, owing, no doubt, to the fact that some centres succumb under its influence before others.

IV. *Certain Preliminary Considerations.*

As marked differences are known to exist in the peripheral laryngeal apparatus in animals according to their age and the precise stage of narcosis at which Faradic excitation of the recurrent laryngeal nerves is employed, it appears to me of primary importance that in any investigation of the condition of the central apparatus of a given animal, we should have some idea whether such differences in the peripheral apparatus can in any way influence the effects obtained from the central apparatus. For without such knowledge differences may be wrongly attributed to the central apparatus which in reality depend on peripheral conditions. It will, I take it, not be denied that the cortical "sensorimotor" centre, excitation of which results in adduction of the vocal cords may be well developed and capable of responding most satisfactorily to stimuli, and yet no closure, or only feeble closure of the glottis may result, not because there is not a sufficient discharge of nerve force from the cortex, but either because the muscles on which this force is expended are incapable of responding properly to it, or because the nerve fibres which transmit this force are incapable of doing so properly from some cause or other. These considerations have led me to adopt the plan, in one series of experiments, of first exciting each intact recurrent laryngeal nerve in the neck with an induced current just strong enough to evoke a response from the muscles of the larynx in the manner already explained. Having ascertained whether such excitation resulted in abduction or adduction of the vocal cords, I next proceeded in one series of experiments to test the condition of the

centres in the cerebral cortex, so as to ascertain whether the peripheral condition influenced the effect obtained from the central mechanism. In testing the condition of the peripheral apparatus a point of some importance was observed, which proves that the result of excitation of one recurrent laryngeal nerve is not necessarily any criterion as to the result which would be obtained by excitation of its fellow even at the same stage of ether narcosis, for under such circumstances I have observed abduction of one cord and adduction of the other. Further, in an animal both of whose cords have been adducted in superficial narcosis, I have seen abduction of the one and adduction of the other in an intermediate stage of narcosis on excitation of their respective recurrent laryngeal nerves.*

In another series, in an animal excitation of whose recurrent laryngeal nerves resulted in adduction of the vocal cords, the adductors were separated from the abductor fibres in one of the nerves, and a thread passed carefully round each bundle, so as to allow of their being held apart very gently, while each in turn was excited with a feeble induced current and the respective movements of the cords evoked. The whole nerve was again excited, so as to be sure that one set of fibres was not more damaged than the other in the process of separation. Having satisfied myself that adduction of the vocal cord still resulted on excitation of the nerve, I then divided the adductor fibres transversely. The result of this in all cases where the abductor fibres had not been unduly injured in the process of separation was to place the vocal cord in a position of abduction. I next stimulated the trunk of the recurrent nerve proximally to the seat of section of its adductor fibres, and satisfied myself that further abduction of the vocal cord on that side followed such a procedure, and that there was no longer adduction of the cord as before the adductor fibres were severed.

Having satisfied myself on this point, I next explored the cerebral cortex in order to ascertain whether this preliminary procedure had effected any alteration as regards the results to be obtained on excitation of the central mechanism.

The cerebral cortex was, therefore, stimulated under the following circumstances.

(a.) *Both Recurrent Laryngeal Nerves Intact.*—Excitation of the cerebral cortex with the induced current under these circumstances gave results in harmony with those obtained by HORSLEY and SEMON,† except that in some instances abduction of the vocal cords could be obtained in the dog in addition to adduction, and that in the cat an additional abductor centre was found, corresponding in position somewhat closely to that of the centre from which abduction was obtained in the dog. Certain other new points, the outcome of these experiments, will be detailed later.

Considerable attention was paid to the question of unilateral representation of the

* I have tried to eliminate any fallacy by raising the nerves well out of the wound at the time of excitation, and I have placed the electrodes on all parts of the circumference of the nerves with the same result.

† *Loc. cit.*

vocal cords in the cerebral cortex as described by MASINI,* but the most careful observation failed to detect any sign of what might be considered unilateral movement of the vocal cords; in every instance the effect of stimulating the adductor centre in the cortex of either cerebral hemisphere appeared to be a perfectly bilateral movement of the vocal cords, resulting in closure of the glottis, nor could one cord ever be said to commence to move before its fellow when the stimulus was applied to the cortex; indeed, the behaviour of the two cords appeared to be in every way identical.

(b.) *One Recurrent Laryngeal Nerve Intact and the other Divided.*—In order to test the question of unilaterality of representation further, it seemed to me that this procedure was absolutely necessary. With only one vocal chord in action then, both cerebral hemispheres were explored, and it was found that the cord whose nerve was intact could be influenced equally well from either cerebral hemisphere, the movement of adduction resulting when the adductor centre was excited.

(c.) *The Adductor Fibres alone Divided in one Recurrent Laryngeal Nerve.*—It was under these circumstances that I first found any evidence of the representation of abduction of the vocal cords in the cerebral cortex of the dog. Under favourable circumstances it is possible to evoke both adduction and abduction on excitation of the respective centres in either hemisphere, the only difference being that whereas both cords participate in the abduction, only that the adductor fibres of whose recurrent laryngeal nerve were intact was responsible for narrowing the aperture of the glottis by its movements of adduction.

(d.) *One Recurrent Nerve completely Divided, and the Adductor Fibres alone Divided in the other.*—Such a procedure enabled me to ascertain, under favourable circumstances, that abduction of the cord whose recurrent laryngeal nerve contained intact abductor fibres could be elicited on excitation of the proper centre in either cerebral hemisphere.

(e.) *The Adductor Fibres Divided in both Recurrent Laryngeal Nerves.*—Provided that the abductor fibres had escaped injury on both sides, the glottis was widely open after this procedure, but excitation of the abductor centre resulted in still wider opening of the glottis. But this preliminary method was adopted more especially with a view to test the question of inhibition of muscular action by cortical excitation.

SHERRINGTON† has shown that it is possible to inhibit an antagonistic muscle by excitation of the cortical area of a muscle responsible for a given movement. Thus, after section of the nerves responsible for the supply of those ocular muscles which turn the eyes to the left, for instance, the eyes may be somewhat inclined to the right owing to the unantagonised tonus of the muscles which normally turn them in this direction, and he found that by exciting the “eye-area” of the right cerebral hemisphere, normally responsible for turning the eyes to the left, such a movement

* *Loc. cit.*

† SHERRINGTON, ‘Proc. Roy. Soc.,’ 1893.

up to the middle line resulted. In view of the fact that the muscles responsible for this movement were no longer connected with the central nervous system, the only way in which such a movement of the globes could result was by a relaxation of the intact muscles which tended to draw the eyes to the right before the cortex was excited.

Now it appeared to me that the larynx would prove a favourable field in which to test this inhibition of muscles on cortical excitation. Accordingly, in animals the adductor fibres of whose recurrent nerves had been previously severed, I applied induced currents of varying strengths to the adductor centre in the precrucial gyrus, and found that with strong currents the cords were arrested in the expiratory phase of their excursions, but that there was no adduction beyond this point. To make my meaning clear it is necessary for me to explain that when the adductor fibres are divided in both recurrent nerves the cords, though abducted by the tonus of the abductor muscles are further abducted slightly at each inspiratory effort, but, during the expiratory phase, they return to a position of less abduction, but, of course, the glottis is much wider open at this stage than when the adductor fibres are intact. Now, it is in this expiratory phase, or one of less abduction, that the cords are arrested in when the adductor centre is excited.*

This may mean that the abductors are inhibited to a certain degree; but if due to inhibition it would not be unreasonable to expect further relaxation of the abductor tonus allowing possibly of the cords assuming the cadaveric position.

Another possible explanation of the phenomenon, and one which cannot as yet be excluded, is the possibility that, owing to the very strong currents necessary, it may be brought about by diffusion of the current to SPENCER'S area of arrest of respiration, from which we shall see later that it is possible to arrest the movements of the vocal cords. I am inclined to believe that this is the true explanation, and that I cannot claim to have in any way induced a degree of relaxation of abductor tonus at all compatible with what might be expected if the excitation of the adductor centre had been the means of inhibiting the abductor muscles of the vocal cords.

I now propose to give in detail the results which were obtained on excitation of different areas of the cerebral cortex in the dog and cat, commencing with the former animal, and to indicate the position of the different foci on the surface of the hemisphere. It has not been possible to publish tracings illustrating all the effects described in this Paper, but a tracing of each effect is preserved in the Archives of the Society.

V. *The Dog.*

1. *Adduction of the Vocal Cords.*—My results are in perfect harmony with those of KRAUSE† and of HORSLEY and SEMON,‡ who found that the chief focus in the cortex, excitation of which resulted in adduction of the vocal cords, was situated in

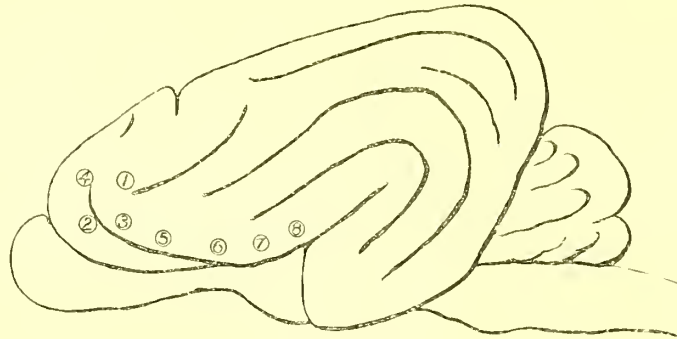
* It must be clearly understood that the extent of movement of the cords referred to under these circumstances was exceedingly small, so that the differences of position were also small.

† *Loc. cit.*

‡ *Loc. cit.*

the præcrucial gyrus, just where it terminates in the narrow isthmus which connects it with the anterior composite gyrus. The more extensive representation of the movement to a slighter extent, with this point as a focus, as described by the latter observers, has also been confirmed by my experiments. The chief focus for this movement is represented in fig. 1, and a graphic record of the movement obtained in the

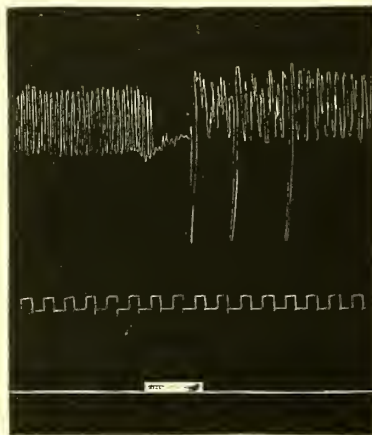
Fig. 1.



Left cerebral hemisphere of the dog. 1 = adductor centre. 2 and 3 = abductor centre. 4 = acceleration. 5 = clonic adductor effect. 6 = arrest in adduction. 7 = arrest in abduction. 8 = intensification and acceleration.

manner already described is shown in fig. 2. The three long strokes seen in the tracing after the stimulus was removed from the cortex represent movements of the recording lever produced each time the animal swallowed. Apart from these

Fig. 2.



Adduction of the vocal cords.

swallowing movements, the tracing shows well how irregular the movements of the vocal cords were immediately after the stimulus was removed from the cortex, as compared with the perfect regularity of rhythm of their movements before the cortex was excited. The irregular rhythm was always temporary, however, and after a

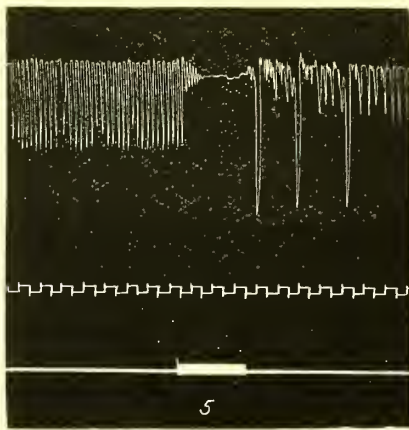
variable interval the cords moved with as great regularity as they did before any stimulus was applied to the cortex.

2. *Abduction of the Vocal Cords.*—In some dogs abduction of the vocal cords was obtained on cortical excitation with the recurrent laryngeal nerves intact, but in others the results were not satisfactory, as only feeble abduction resulted, and the centre on which the movement depended appeared to be very quickly exhausted. But the majority of the dogs examined in my earlier experiments presented no evidence of the possibility of evoking this movement of abduction of the vocal cords on excitation of the cerebral cortex, while the adductor fibres were intact in both recurrent laryngeal nerves. It was quite otherwise, however, when the adductor fibres had been divided in one recurrent laryngeal nerve before the cerebral cortex was explored. Under favourable circumstances this procedure seldom failed to make it possible to evoke unquestionable abduction of both vocal cords on excitation of a limited focus on the prorean gyrus just in front of and below KRAUSE's adductor centre already described, the two foci being separated by the supra-orbital sulcus. The resulting movement of abduction appeared to be bilateral and was obtained on excitation of either cerebral hemisphere, irrespective of the side on which the adductor fibres in the recurrent laryngeal nerve had been divided. This movement of abduction, as evoked from the cortex, could also be demonstrated when the adductor fibres in both recurrent laryngeal nerves were divided, but this was less satisfactory owing to both cords being already somewhat far apart. Division of the adductor fibres in only one recurrent laryngeal nerve had the further advantage of allowing adduction of the vocal cord whose recurrent nerve was wholly intact to be obtained at the time that abduction of both cords was being obtained, *i.e.*, at the same stage of ether narcosis. It was then found that at a given time, when the animal was not too profoundly under the influence of the anaesthetic, it was possible to evoke adduction of the vocal cord whose recurrent nerve was intact by excitation of the lower end of the præcrucial gyrus, and abduction of both cords on excitation of the prorean gyrus in front of and below this last point. After what has been insisted on with regard to the influence of the anaesthetic in vitiating the results obtained, it will be readily understood how exceedingly important it is that it was possible to demonstrate both the movement of adduction and that of abduction on excitation of the cerebral cortex when the animal was in precisely the same stage of ether narcosis.

In my later experiments in which I have been able to evoke well marked abduction of the vocal cords on excitation of the cerebral cortex in dogs whose recurrent laryngeal nerves were intact, the focus from which the movement could be best obtained was on the anterior composite gyrus just behind the supra-orbital sulcus and below the level of the imaginary prolongation of the coronal sulcus, to touch the supra-orbital sulcus (see fig. 1). This appears to be the true focus for abduction, and is situated just posterior to that from which I first obtained the movement when the

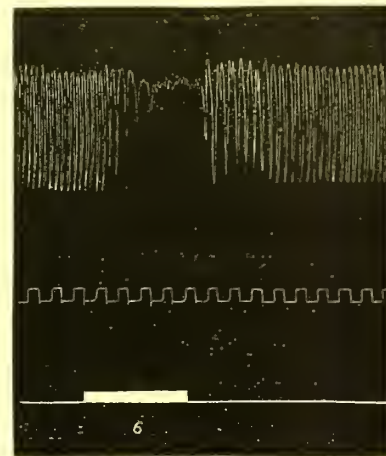
adductor fibres in one recurrent laryngeal nerve had been previously divided, the two points being separated by the supra-orbital sulcus, but otherwise close together. Fig. 3 represents a tracing of the movements of the vocal cord in a dog, the adductor fibres of one of whose recurrent laryngeal nerves had been divided before the cortex was excited, and shows how the regular rhythm and extent of the excursions of the cords was altered after the stimulus was removed from the cortex. The three deep excursions of the lever were the results of swallowing movements on the part of the animal. In fig. 4, which is a record of abduction of the vocal cords in an animal both of whose recurrent laryngeal nerves were perfectly intact, the regular rhythm of the movements of the cords was much less disturbed by the excitation, and no swallowing movements resulted.

Fig. 3.



Abduction of the vocal cords in an animal with the adductor fibres divided in one recurrent laryngeal nerve.

Fig. 4.



Abduction of the vocal cords in an animal with both recurrent laryngeal nerves intact.

3. *Acceleration of the Movements of the Vocal Cords* I have sometimes found best marked at the point on the præcrucial gyrus which HORSLEY and SEMON* considered the chief focus, while at other times it was best obtained from the upper end of the supra-orbital sulcus, the point which SPENCER† considered the chief focus for acceleration of respiration.

This acceleration is well shown by the graphic method, and it may be seen from such tracings that during the time that the movements of the vocal cords were more rapid, the extent of their excursions was slightly less than before and after the stimulus was applied to the cortex. The rhythm of the movements of the cords was only very slightly disturbed after the stimulus was discontinued in some instances.

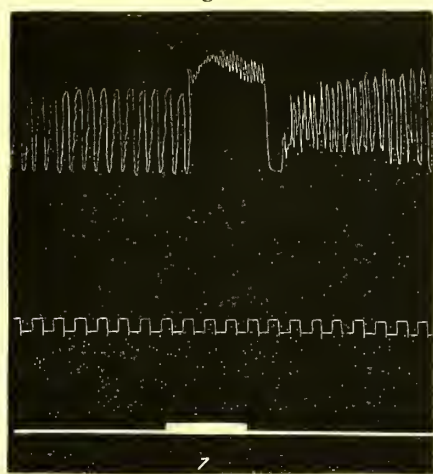
In some dogs it is not easy to obtain acceleration without some admixture of

* *Loc. cit.*

† *Loc. cit.*

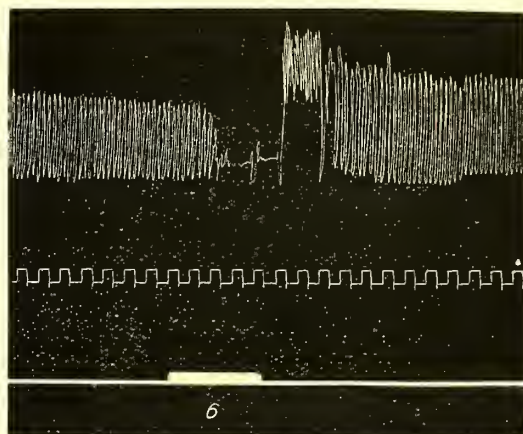
abduction, or to obtain abduction without some acceleration being added, so that in either case a double effect results. Even when the two effects can be separated by excitation of their respective foci in the cerebral cortex, it is usually possible to obtain the combined effect by exciting some focus intermediate between the two points where each movement is best represented. This combination of the two effects is well shown in fig. 5 where, with well-marked abduction of the vocal cords, there is in addition distinct evidence of acceleration of their movements in this abducted condition. In this instance the abduction is the chief effect and the acceleration less pronounced; but I have in my possession tracings in which the acceleration is the chief effect and the abduction much less obvious than in fig. 5.

Fig. 5.



Abduction and acceleration of the movements
of the vocal cords.

Fig. 6.

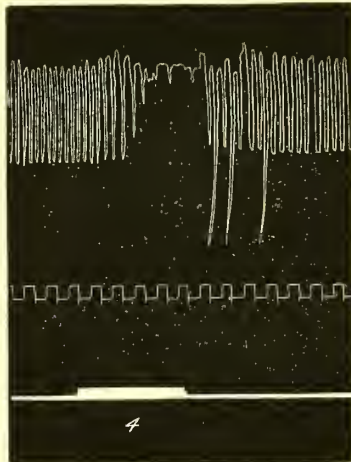


Arrest of the vocal cords in adduction.

4. *A Clonic Adductor Effect on the Cords.*—This effect consisted in an adduction of the vocal chords beyond the position they assume in the expiratory phase of respiration, after which further interrupted adductor movements of the cords were added in quick succession, giving rise to a sort of clonic effect, in which, after each adductor effort, the cords returned to the position of adduction greater than that of the expiratory phase of quiet respiration. This condition was met with on excitation of the anterior composite gyrus just behind the supraorbital sulcus and just below the anterior tip of an imaginary prolongation of the anterior suprasylvian sulcus to touch the supraorbital (see fig. 1). This was the focal point of this effect, which was, however, also obtained from a limited area around this on the anterior composite gyrus. It will thus be seen that the area from which these movements of the cords were obtained is below that, excitation of which resulted in abduction of them. That this effect is a totally distinct one from that described by SPENCER as the snuffing movements in connection with the respiratory movements of the thorax, may be seen by examining fig. 8, which is a record taken from the larynx when SPENCER's snuffing

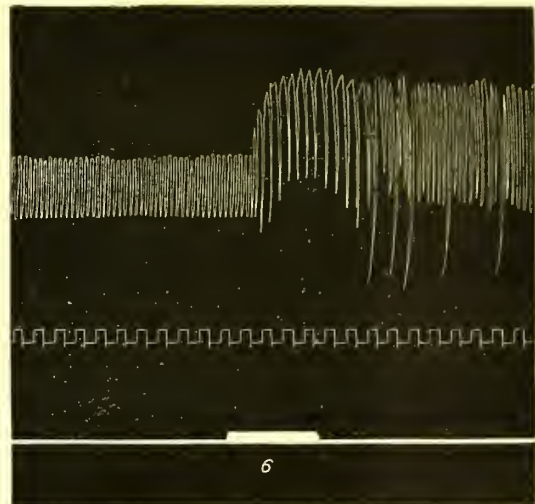
effect was elicited on excitation of the olfactory bulb. It may readily be seen that this differs from the effect I have just described, in that there is no tonic adduction phase about it, but on the contrary an abductor tendency, and that after each adductor effort the cord returns not only to the abductor phase of ordinary respiration, but to one of more active abduction. The two effects then are totally different, besides which an area of cortex, from which neither effect can be obtained, separates the respective foci from each other. Although what I have described with regard to what I have called the clonic abductor effect is what could actually be seen when the vocal cords were under observation when this particular area of the cerebral cortex was excited, yet from the tracings it was obvious that some other effect was being obtained also as shown by the depth of descent of the

Fig. 7.



Arrest of the vocal cords in abduction.

Fig. 8.



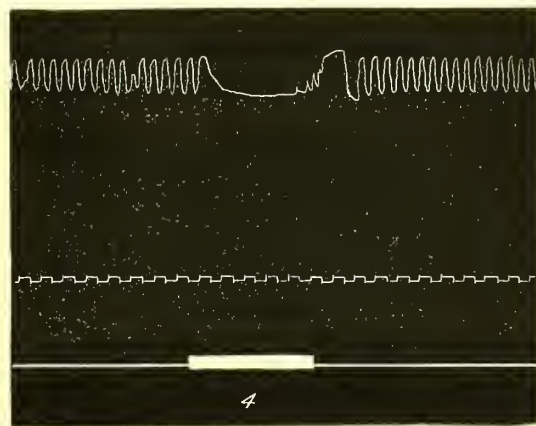
Effect on the vocal cords during snuffling movements.

lever, but what the exact effect on the pharynx or any adjacent part was, it was impossible to determine. This much is however certain, viz., that the regularity of the rhythm of the cords was more disturbed after excitation of this area than after any other, and that a great many more swallowing movements followed the removal of the stimulus from the cortex. Records from the same animal, in about the same stage of ether narcosis, showed a difference in the effect obtained according to the strength of the stimulus employed; with a stronger stimulus the cords were held more in a tonic state of adduction, there being much less of the clonic effect added, while with a weaker stimulus the clonic effect was much more obvious.

5. *Arrest of the Vocal Cords in Adduction.*—This consists in an arrest of the cords in the position they occupy during the expiratory phase of quiet respiration (see fig. 6), there being no active adduction of them beyond this point as in the effect last

described. The focus from which it can be obtained is on the anterior composite gyrus just behind the angle where the lower end of the supraorbital sulcus joins the rhinal (see fig. 1). It is not as a rule easy to separate this effect in the dog from that just described, and from that of arrest in abduction which will next be described ; but in the cat, as will subsequently be seen, this focus for arrest in adduction is easily separated both from the focus for the clonic adductor effect and from that for arrest of the cords in abduction. The effect is best obtained when the animal is moderately under the influence of ether, as, in common with the focus for arrest in abduction, in deeper narcosis slowing of the movements of the cords can alone be obtained.

Fig. 9.



Arrest of the vocal cords in adduction from SPENCER'S area
for arrest of respiration.

6. *Arrest of the Vocal Cords in Abduction.*—The focus on the anterior composite gyrus just behind that last dealt with is the one excitation of which results in arrest of the cords in abduction. It is situated just below the level of the anterior end of the anterior ecto-sylvian sulcus (see fig. 1) and corresponds closely to the focus from which HORSLEY and SEMON obtained abduction of the vocal cords in the cat. When this focus is stimulated the vocal cords are arrested in abduction, as is shown in fig. 7, a tracing taken under such circumstances. It is an effect more readily obtained than the last, but like it can only be evoked in a stage of moderate ether narcosis, as excitation of the same area in deeper narcosis results in slowing of the movements of the cords, or arrest in adduction, according to the precise degree of narcosis.

7. *Intensification and Acceleration of the Movements of the Vocal Cords.*—This is not nearly so easy to demonstrate in the dog as compared with the cat, owing to the fact that the movements of the dog's cords are as a rule very energetic, except in the deeper stages of narcosis. This being the case, in order to show the effect well in dogs, it is as a rule necessary to place the animal as deeply under the influence of ether as is necessary to obtain slowing of the movements of the cords on excitation of

the two areas last described. Thus, in deep ether narcosis, at a stage in which excitation of both the area for arrest in adduction and that for arrest in abduction usually results in slowing of the movements of the cords, excitation of this focus, which is immediately behind that for arrest in abduction, was responsible for distinct intensification of the movements of the vocal cords, together with acceleration sometimes. The intensification is accompanied by acceleration, if narcosis is not too profound, and the exact focus from which the effect is as a rule best obtained is about the point of junction of the anterior sylvian and anterior composite gyri (see fig. 1).

8. SPENCER'S *Area of Arrest of Respiration*.—Provided the animal be sufficiently under the influence of ether, or if ether and morphia narcosis be combined, excitation of the chief focus of this area results in arrest of the movements of the vocal cords in the adductor position of the expiratory stage of respiration (see fig. 9), a fact in keeping with the result obtained by SPENCER with regard to respiration, for he found that in the dog excitation of this area resulted in arrest of respiration in expiration. This focus is on the olfactory lobe, with the olfactory tract and rhinal fissure bounding it in front and laterally, and with the sylvian artery behind, forming the base of the triangular area of grey matter.

Instead of the movements of the vocal cords being arrested, they were sometimes only slowed, an event consequent on one of the following causes: an insufficient amount of the anæsthetic, too much anæsthetic, or, with the proper degree of anæsthesia, an insufficient strength of Faradic current.

VI. *The Cat.*

The same preliminaries were gone through in cats as in dogs in attempting to ascertain the condition of the peripheral laryngeal apparatus during moderate narcosis, before the cortical areas were stimulated.

As in the dog, no difficulty was encountered in adjusting the current to such a strength as to elicit movement of the vocal cord whose intact recurrent laryngeal nerve was excited, without producing any effect on the opposite vocal cord. In some cats the resulting movement of each cord, when its corresponding recurrent nerve was excited, was that of adduction, in others, it was abduction; while in a few, at the same stage of ether narcosis, abduction of one cord resulted when its nerve was stimulated, while adduction of the opposite cord followed excitation of its nerve.

In accordance with what was found in the dog, the peripheral condition appeared to in no way affect the results obtained on cortical excitation, for in animals whose cortical centres responded to the stimulus adduction could be obtained on excitation of the appropriate area, even in an animal excitation of whose recurrent laryngeal nerves had resulted in abduction of the cords. So too stimulation of the centre for abduction resulted in that movement in animals whose cords were adducted on excitation of the recurrent laryngeal nerves.

1. *Adduction of the Vocal Cords*.—My results with regard to this movement quite agree with those of HORSLEY and SEMON in this respect, and, like these observers, I found that the most usual focus from which it could be evoked was on the coronal

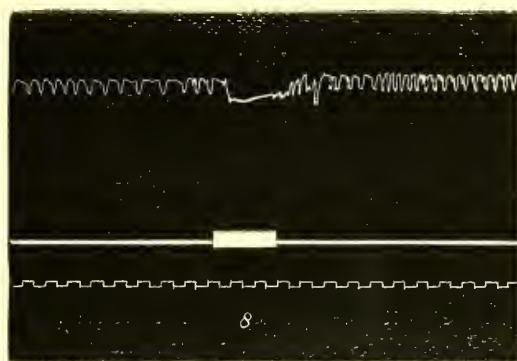
Fig. 10.



Left cerebral hemisphere of the cat. 1 = adductor centre. 2 = abductor centre. 3 = acceleration. 4 = clonic adductor effect. 5 = arrest in adduction. 6 = arrest in abduction. 7 = intensification and acceleration.

gyrus near its anterior end where it joins the anterior composite gyrus (see fig. 10); but in a few instances the movement was best obtained from the area corresponding to KRAUSE's phonation centre in the dog, viz., just above and in front of the anterior end of the coronal sulcus. Fig. 11 represents a tracing of this movement of the

Fig. 11.



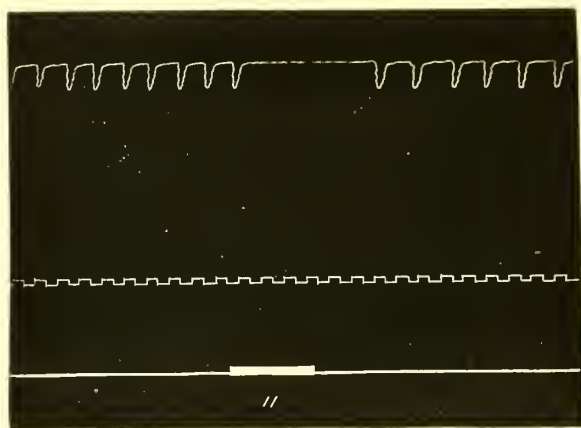
Adduction of the vocal cords.

vocal cords, and it may be seen that the rhythm of the movements of the cords was not regular before the stimulus was applied to the cortex, but that it became still more irregular immediately after the stimulus was discontinued.

2. *Abduction of the Vocal Cords*.—Following the plan already detailed in connection with my first attempts to obtain this movement in the dog, I divided the adductor fibres in one recurrent laryngeal nerve before exciting the cerebral cortex. Excitation of the cortex under these conditions showed that there was a focus on the prorean gyrus, closely corresponding to the position of that described in the dog, excitation of which resulted in abduction of the vocal cords; and in

subsequent experiments it became evident that no such preliminary procedure as that of dividing the adductor fibres of one recurrent laryngeal nerve was necessary to allow this movement to be obtained. With both recurrent nerves intact, abduction could be obtained from the focus in question with the greatest constancy, in nearly

Fig. 12.



Abduction of the vocal cords.

all cats, when the cerebral cortex as a whole was excitable. This movement could always be best obtained from the prorean gyrus in front of, and below the level of, the adduction centre, which corresponds to KRAUSE's phonation centre in the dog, *i.e.*, it is in front of, and below the level of, the anterior end of the coronal sulcus, and is separated from it by the supraorbital sulcus (see fig. 10). As a rule the strength of the current can be so regulated as to elicit this movement alone, as is shown in fig. 12, in which case not even the regular rhythm of the movements of the cords was disturbed after the stimulus was removed from the cortex, as we have seen to be so common in connection with the evoking of other movements of the cords. But when the movement of abduction is complicated by the simultaneous occurrence of any other effect on the cords, it was always acceleration of their movements, so that with the cords in an abductor position short rapid excursions of them continued as long as the stimulus lasted. This resulted especially when the stimulus happened to be applied between the chief abductor focus and the upper end of the supraorbital sulcus, from which latter point, as we shall immediately see, acceleration of the movements of the cords, without abduction, can be obtained.

3. *Acceleration of the Movements of the Vocal Cords* was found closely associated with the movement of abduction, as has just been explained, being obtained on excitation of the prorean convolution just at the upper end of the supra-orbital sulcus (see fig. 10). This corresponds with the focus for acceleration of respiration as described by SPENCER. In many cats it was impossible to obtain a record of acceleration uncomplicated by abduction, even when this the chief focus for accelera-

tion was stimulated, but in some it was possible to differentiate this effect from that of abduction.

4. *A Clonic Adductor Effect on the Cords*.—As in the dog, so in the cat, this effect consisted in an adduction of the vocal cords beyond the position they occupy in the expiratory phase of respiration, though not so much as to close the glottis, to which were added further rapid interrupted adductor movements, giving rise to a clonic effect, in which the cords, though adducted, rapidly moved backwards and forwards. This effect was obtained from the same area as in the dog, viz., the anterior composite gyrus just behind the supra-orbital sulcus, and just below the imaginary prolongation of the anterior extremity of the anterior supra-sylvian sulcus to touch the supra-orbital sulcus (see fig. 10). In some instances the area appeared to extend downwards and backwards so as to overlap that from which the next effect to be described was obtained. Tracings of this effect showed that the regular rhythm of the movements of the cords was greatly disturbed after the stimulus was removed from the cortex. Records of the movements of the cords during snuffing, as obtained on excitation of the olfactory bulb, showed that it is totally different from the effect just described.

In some cats, as is well known, the vocal cords are held in abduction even in comparatively superficial narcosis, and even in such an animal it is possible to demonstrate this effect, which I have called a clonic adductor effect, on excitation of the proper focus on the anterior composite gyrus. In such a case, after the stimulus is removed from the cortex, a few irregular jerky movements of the vocal cords occurred, and they then once more returned to their former position of abduction.

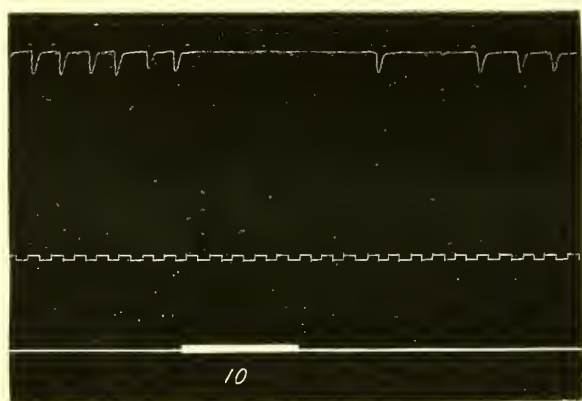
5. *Arrest of the Vocal Cords in Adduction*.—Here instead of there being an adduction of the cords beyond the position they occupy in the expiratory phase of quiet respiration, they were simply arrested in the adductor position which they normally assume in the expiratory phase of respiration. This condition of things could only be brought about when the animal was not too deeply under the influence of ether, for when that was the case, though the excitability of the cortex was not abolished, the only result to be obtained from this and other contiguous areas was arrest of the cords in abduction. But even when the narcosis was not too deep it was sometimes difficult to separate this effect from the last described, whose area of representation apparently sometimes overlapped that from which the arrest in adduction was obtained. The focus excitation of which resulted in this arrest was on the anterior composite just behind the angle where the lower end of the supra-orbital sulcus and the rhinal fissure meet, i.e., slightly below the point where an imaginary prolongation of the anterior extremity of the anterior ecto-sylvian sulcus would touch the supra-orbital sulcus (see fig. 10).

6. *Arrest of the Vocal Cords in Abduction*.—This resulted both when the animal was in the proper stage of narcosis to allow the last effect to be obtained, and also when it was so deeply under the influence of ether that only arrest in abduction

could be obtained from this and contiguous areas. The focus is situated behind that which has just been described, and evidently corresponds to the focus from which HORSLEY and SEMON evoked abduction of the vocal cords in the cat; for it is on the anterior composite gyrus above the rhinal fissure and below the depression representing the antero-ecto-sylvian sulcus (see fig. 10).

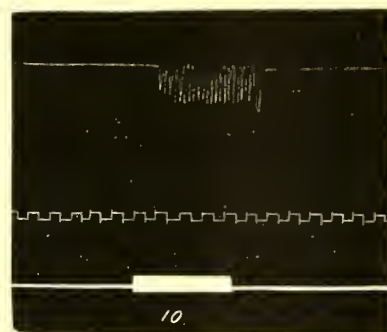
7. *Intensification and Acceleration of the Movements of the Vocal Cords.*—This is an effect which is much easier to demonstrate in the cat than in the dog, as normally, under a moderate amount of an anæsthetic, the movements of the cat's vocal cords are less vigorous than those of the dog, under similar circumstances. The area from which this double effect can be obtained is situated behind the last focus described, just above the junction of the anterior sylvian gyrus with the anterior composite, and extending somewhat on to the anterior sylvian gyrus, in front of the sylvian artery (see fig. 10). Sometimes the one, sometimes the other effect was the more marked on excitation of this area of the cortex, but, as a rule, the combined effect of intensification of the movements with acceleration was that obtained. Like the arrest

Fig. 13.



Arrest of the vocal cords in abduction, from SPENCER'S area for arrest of respiration.

Fig. 14.



Intensification and acceleration of the movements of the vocal cords in an animal whose cords were in abduction before the cortex was excited.

of the cords in adduction, this effect could only be obtained when the animal was not too deeply under the influence of ether, since in the deeper stages of narcosis, in which the cortex was still excitable, arrest of the cords in abduction was obtained from the area, as from all adjoining areas in the same stage of narcosis. It will thus be seen that, while in the dog it is necessary to make the movements of the cords less energetic, by putting the animal rather deeply under the influence of ether, in the cat, whose cords are, as a rule, very much less vigorous in their movements, the effect can be best obtained in moderate narcosis. Even in those cats where the cords were constantly kept in a position of abduction regardless of the stage of narcosis, this effect could always be evoked, as is well shown in fig. 14, from which it may be seen that, while the cords were motionless in abduction before the

stimulus was applied to the cortex, excitation of the proper focus immediately resulted in active movements of the cords, which continued as long as the excitation lasted.

8. SPENCER'S *Area of Arrest of Respiration*.—As in the dog, so in the cat, excitation of this area on the olfactory lobe, between the olfactory tract and rhinal fissure in front, and with the groove for the sylvian artery bounding it posteriorly, resulted in arrest of the movements of the vocal cords; but, instead of being arrested in the expiratory position, as in the case of the dog, the cords were arrested in abduction, *i.e.*, the position which they occupy in the inspiratory stage of respiration (see fig. 13), a fact in keeping with SPENCER'S results, for he found that excitation of this area in the cat resulted in arrest of respiration in inspiration as a rule.

What has been said with regard to slowing of the movements of the cords in the dog holds good for the cat also, and need not be repeated here.

VII. *Discussion of Results.*

The results of excitation of the recurrent laryngeal nerves make it obvious that the effect produced on the vocal cord by excitation of this nerve on one side is no absolute criterion as to the effect which may be obtained on excitation of the opposite nerve in the same animal at the same stage of ether narcosis. As a rule the result obtained on excitation of one recurrent nerve is the same as that obtained on excitation of its fellow, provided they be both stimulated when the animal is as nearly as possible in the same stage of ether narcosis; but we have seen that in a few animals, in spite of the stage of narcosis, the strength of current and the frequency of its interruptions being the same, abduction may be obtained on stimulating one recurrent nerve, while adduction results on excitation of the other.

On comparing the effects obtained in the larynx, when the centres governing the movements of the vocal cords are stimulated in the cerebral cortex, with the effects obtained, in the same animal, on exciting the recurrent laryngeal nerves, it becomes clear that the condition of the peripheral laryngeal apparatus does not influence, at any rate to any marked degree, the results produced in that apparatus by cortical excitation. Adduction and abduction of the vocal cords were obtained on stimulating the respective centres on which these movements depend both in animals excitation of whose recurrent laryngeals resulted in adduction of the vocal cords, and in others in which a similar procedure was attended by abduction of them. This does not exclude the possibility that the condition of the peripheral apparatus may influence or modify the effect of the cortical excitation, but it nevertheless proves that the cortical effect is largely independent of the condition of the peripheral apparatus, provided, of course, that the peripheral apparatus is intact.

With regard to the question of the representation of the movements of abduction and adduction in the cerebral cortex, my results point to somewhat different con-

clusions to those arrived at by HORSLEY and SEMON* in their researches in this direction. Our results are in accord as far as the representation of the movement of adduction is concerned in the cat and dog; but it is otherwise with regard to the question of the cortical centre for abduction of the vocal cords. It is true that these observers like myself obtained abduction of the vocal cords on excitation of the cerebral cortex in the cat: but my results point to the focus from which HORSLEY and SEMON obtained abduction as probably the focus for arrest of the vocal cords in abduction which probably accompanies the arrest of the respiratory movements of the thorax described by SPENCER. This conclusion is suggested to me by the following considerations. Well-marked abduction of the vocal cords can also be obtained from quite a different area in the cortex from that from which HORSLEY and SEMON obtained it. Further, the area for acceleration of respiration is that situated nearest to the focus on the prorean gyrus from which I obtained abduction of the vocal cords; whereas the proximity of SPENCER's chief focus for the arrest of respiration makes it possible for an effect obtained from HORSLEY and SEMON's abductor centre to be in reality due sometimes to spread of the current to the arrest centre, and, apart from this, the focus for abduction as indicated by these observers comes within the peripheral limits of the arrest area as defined by SPENCER, and comparable to the other focus within SPENCER's area of arrest of respiration from which arrest of the cords in adduction can be obtained, rather than a centre for abduction comparable to that for adduction which they found on the coronal gyrus in the cat.

The fact that I have obtained evidence of the existence of a focus in the cerebral cortex of the dog, excitation of which results in abduction of the vocal cords, is at variance with the results obtained by HORSLEY and SEMON in this animal, for they were unable to find any evidence of the existence of such a focus. That this should have been their experience is in no way surprising, for I feel sure that but for the preliminary procedure of dividing the adductor fibres in one recurrent laryngeal nerve before exciting the cortex, which enabled me to find the first indications of the existence of such a focus, my conclusion would have been the same as theirs. It was only after I had divided the adductor fibres in one or both recurrent laryngeal nerves that I was able to evoke the movement of abduction of the vocal cords, by stimulating the particular focus on the prorean gyrus. This, of course, led me to test the excitability of this portion of the cortex with still greater care, in all stages of ether narcosis, even in animals whose recurrent laryngeal nerves were both intact, with the result already detailed. That abduction is not so readily obtained as adduction in the dog, no doubt means that the latter movement of the vocal cords is so much more powerfully represented in the cerebral cortex that it is difficult to find a stimulus strong enough to evoke abduction, and yet delicate enough not to bring out the preponderating adductor influence, which, if not actually resulting in adduction of

* *Loc. cit.*

the vocal cords, may yet be sufficient to prevent the abductor influence from showing itself in an actual movement of abduction. Another explanation of the condition of affairs might be, that the adductor influence constantly exerted on the vocal cords is so great that it cannot be overcome by the abductor impulse originated in the cerebral cortex on electrical excitation. The former of these explanations appears the more probable, however, when compared to the condition met with in connection with the cortical representation of eye movements, for in that case there could be no question that the representation of the lateral movements of the eyes was so powerful, that it was impossible to evoke the simple upward and downward movements of the globes until it had been made impossible for these lateral movements to take place by division of the lateral recti responsible for their production.

That the focus that has thus been eliminated in the anterior composite and prorean gyri is probably the true abductor cortical centre for the vocal cords, is made more likely by the fact that it is precisely in the same region in the cat's brain that this effect is to be obtained. The only difference being that in the cat abduction of the cords can always be evoked on cortical excitation whether the adductor fibres in the recurrent laryngeal nerves be intact or not, whereas in the dog it is sometimes necessary to divide the adductor fibres in one recurrent nerve before it is possible to elicit abduction on exciting the cortex. This would appear to signify that in the cat the cortical centres for abduction and adduction are more equally balanced, and that there is not the preponderance of the adductor centre over the abductor as in the case of the dog ; in fact there is rather a preponderance of the abductor over the adductor.

The relative position which I have ascribed to the abductor centre, as compared with the adductor, is in accord with the results which HORSLEY and SEMON obtained on exciting the fibres of the internal capsule, for they place the fibres, excitation of which gave rise to abduction of the vocal cords, in front of those which, when excited, resulted in adduction of the cords. That these observers found such fibres in the internal capsule of the dog and monkey, as well as in the cat, excitation of which evoked adduction of the vocal cords, appears to me to be strong presumptive evidence that a focus exists in the cortex of the dog and monkey, as well as in the cat, excitation by which is responsible for abduction of the vocal cords. How are we to otherwise explain the presence of these excitable fibres in the internal capsule which, when stimulated, resulted in abduction of the cords ?

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